TAXONOMIC INTERRELATIONSHIPS IN THE QUERCUS DUMOSA COMPLEX

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The most perplexing taxonomic problems in the Californian oaks have centered around the highly variable scrub oak, *Quercus dumosa* Nutt., and its closest relatives. The interpretation and taxonomic status of certain of these entities have varied widely with different authors. One major factor contributing to the difficulty has been the lack of sharply defined genetic barriers between these oaks. In one part or another of its range, *Q. dumosa* evidently intergrades to a greater or lesser degree with several of its relatives: *Q. durata* Jepson, *Q. Engelmannii* Greene, *Q. Macdonaldii* Greene, and *Q. turbinella* Greene. The last-named oak intergrades conspicuously, in turn, with *Q. Douglasii* H. & A.

A study of interrelationships between certain of these oaks has led to conclusions that vary somewhat from the treatments accorded them in current manuals. Since a large part of the results of this study is being published in an essentially non-taxonomic journal (Tucker, in press), it seems appropriate to record the taxonomic conclusions here. The following notes concern *Quercus turbinella* Greene, *Q. dumosa* Nutt., *Q. Alvordiana* Eastwood, and *Q. Douglasii* H. & A. They include the publication of a new subspecies and a new combination, as well as discussions of reasons for the decisions expressed herein.

The writer is indebted to Professors Lincoln Constance and Herbert L. Mason for suggestions and constructive criticism in the preparation of this paper. Thanks are due, also, to the curators of the following herbaria for the loan of specimens; the latter are cited in the text by the abbreviations proposed by Lanjouw (1939, 1941): Arnold Arboretum, Harvard University (A); California Academy of Sciences (CAS); Dudley Herbarium, Stanford University (DS); New Mexico College of Agriculture and Mechanic Arts[1]; Pomona College (POM); San Diego Society of Natural History Herbarium (SD); Sul Ross State College, Alpine, Texas[1]; Utah State Agricultural College (UTC); University of Arizona (ARIZ); University of California, Berkeley (UC); University of California, Los Angeles (LA); and the United States National Museum Herbarium (US). Specimens in the writer's personal collection, not yet assigned to a permanent herbarium, are cited by his initials (JMT).

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[1] No abbreviation proposed by Lanjouw; inasmuch as specimens from these herbaria are not cited herein, no abbreviations are designated.

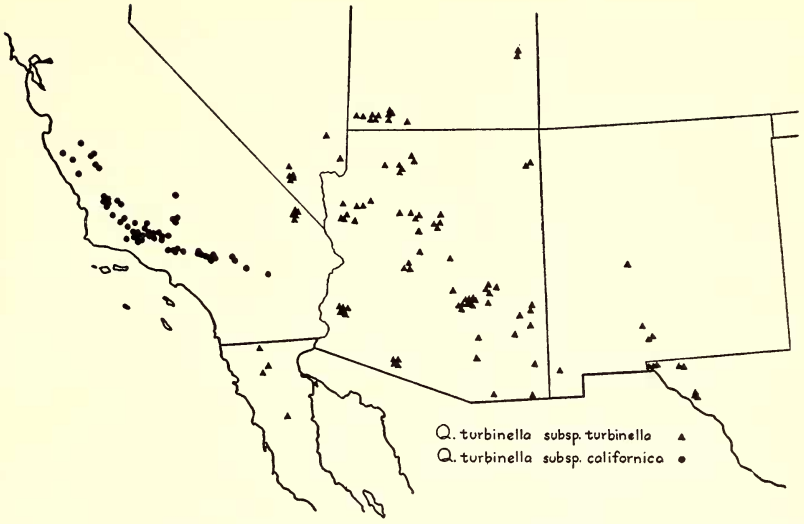

FIG. 1. Distribution of *Quercus turbinella* in southwestern United States and Mexico.

QUERCUS TURBINELLA GREENE

Quercus turbinella was described from specimens collected by G. W. Dunn in Lower California ". . . some twenty or thirty miles below the United States boundary in September, 1888 . . ." (Greene, 1889–90, p. 38). Its history in botanical literature, however, goes back many years earlier. Thus, collections apparently of this oak (Trelease, 1924, pl. 207) made by Fremont on his expedition of 1843–44, were cited by Liebmann in his original description of *Q. berberidifolia* (although Liebmann's type was evidently a specimen of *Q. dumosa* Nutt.). Engelmann was familiar with this shrubby oak, but associated it with *Q. pungens* Liebm., which he treated as a variety of *Q. undulata* (1876–1877; and in Watson, 1880).

Following his original description of *Quercus turbinella*, Greene mentioned that it occurred in the vicinity of Campo, San Diego County (a statement which seems open to question), in addition to the mountains of Lower California. The following year he mentioned having seen a specimen from the borders of the Mojave Desert, and also a similar oak in northwestern Arizona, both of which he considered to be conspecific with his *Q. turbinella* (1889–1890, p. 59). (For the geographical distribution of *Quercus turbinella* as recognized by the present author, see fig. 1.)

Subsequent to Greene's original description, this oak has been accorded various treatments by different authors. Some have considered the Californian and Lower Californian material to be conspecific with that from Arizona and eastward.

Others have treated only the former populations under Greene's name and, implicitly or explicitly, have considered the Arizona material to represent a different species. Some have followed Greene in considering *Quercus turbinella* a species distinct from *Q. dumosa,* others have treated it as a variety of the latter, and still others have not accorded it even varietal status, regarding it as merely a form of the latter.

Two principal questions are apparent in this taxonomic confusion. (1) Are the populations of southern California, Lower California, and Arizona and eastward all conspecific, or are there sufficient grounds for recognizing more than one species? (2) Is *Quercus turbinella* specifically distinct from *Q. dumosa,* or should it more properly be placed in an infraspecific status under the latter? In this study these problems have been considered in some detail.

The Component Elements of Quercus turbinella

As previously mentioned, Greene considered specimens from near Campo, San Diego County, and from the border of the Mojave Desert to be specifically identical with his Lower Californian type. In fact, all subsequent treatments of *Quercus turbinella* seen by the author have borne the implication that the Lower Californian population of the species is simply a southward extension of the population of southern California. Regarding the obviously related shrubs he had observed in northwestern Arizona, Greene at first suspected them to be *Q. pungens* Liebm. and felt that his *Q. turbinella* might possibly have to be regarded as a geographical subspecies of it (1889–90, p. 59). Shortly thereafter, however, having had the opportunity to examine Liebmann's type of *Q. pungens,* Greene concluded (1890) that the Arizona shrubs were "not at all referable" to the latter but represented a "slightly aberrant form" of his *Q. turbinella.*

Later authors have expressed a variety of opinions in regard to the relationship between the populations of Arizona and California. Sargent (1895) regarded the Arizona material as a form of *Quercus undulata* Torr., and the Californian and Lower Californian material as a form of *Q. dumosa.* Neither Jepson (1909, 1910, 1925), Munz (1935), Abrams (1910, 1940), nor McMinn (1939) mentioned the occurrence of *Q. turbinella* (or *Q. dumosa* var. *turbinella* or *Q. dumosa, sensu lato,* depending on the author) to the east of California. From this it is evident that these authors did not include the population of Arizona and eastward in their concept of *Q. turbinella.* One may presume that they associated the eastern material with *Q. undulata* or *Q. pungens* as Sargent and Engelmann had done. Wooton and Standley (1915) listed *Q. turbinella* in their enumeration of the oaks of New Mexico, but expressed the opinion that the specimens they referred to this species might more properly belong to *Q. pungens.* Trelease (1924) recognized that a close

relationship existed between the Arizona population and the populations of southern and Lower California, but he followed Jepson in his treatment of the latter two (as *Q. dumosa* var. *turbinella),* and elevated the former to specific rank, as *Q. subturbinella* Trel.

On the other hand, Tidestrom (1925) and Muller (1940; and in Kearney and Peebles, 1942) made no taxonomic distinction between the populations of southern California, Lower California, and Arizona and eastward, treating them all under *Quercus turbinella.* It may be noted, incidentally, that in the opinion of Muller, contemporary student of southwest American oaks, *Q. turbinella* and *Q. pungens* are not closely related and not even superficially similar (in Kearney and Peebles, 1942).

The pattern of morphological variation exhibited by an extensive series of specimens is correlated with geographical distribution. On the basis of several differences (discussed below) the species population as a whole is clearly divided into eastern and western sub-populations. The latter occupies an area entirely within California, extending from central San Benito County southeastward in the inner South Coast Ranges to the mountain slopes on or near the southern and western borders of the Mojave Desert in southern California. The former occupies an area extending from the Charleston Mountains in southern Nevada, the New York Mountains in eastern San Bernardino County, California, and the higher mountains of northern Lower California, eastward through Arizona to western Texas, and presumably into northern Mexico. Since the type locality is in Lower California, for purposes of comparison the species population in this area will be treated as a third geographical sub-population. Evidently there are geographical discontinuities separating these three sub-populations (fig. 1), although they may be no greater than others existing elsewhere in the range of the species.

In order to elucidate the statements made above, the morphological relationships of the three sub-populations mentioned will now be considered. A comparison of the Californian with the mainly extra-Californian sub-population east of the Mojave Desert will be considered first; these two will then be compared with Greene's type and other collections from Lower California.

Several fairly well-marked morphological differences exist between the Californian and eastern sub-populations, although the magnitude of some of these is rather small. The following tabulation will serve to summarize them. The first five are the most constant, the final two being merely rather strong tendencies. A tendency to differ in the relative thickness of the margin of the accorn cup may be noted in some specimens, also. In the Californian sub-population the cups, as seen in section,

Table 1. Morphological Differences between Eastern and Californian Sub-populations of Quercus turbinella.

Q. turbinella of Arizona and eastward	*Californian Q. turbinella*
1. Spinose dentation of leaf margin often quite regular, the teeth often directed outward and forward.	1. Dentation of leaf margin more or less irregular.
2. Leaf base rounded to cordate, the blade not at all decurrent along the petiole.	2. Leaf base variable—from rounded to cuneate, only rarely cordate, the blade tapering into or often minutely decurrent for a short distance on the petiole.
3. Leaves usually oblong (to ovate) with pointed (spinosely acute to obtuse) apices.	3. Leaf shape variable—elliptical, sub-orbicular, oblong, or ovate, often with more or less rounded apex.
4. Fruit usually distinctly pedunculate.	4. Fruit usually sessile, or nearly so.
5. Nuts usually short (12-23 mm. long), and cylindric-ovoid or -ellipsoid, tapering rather abruptly toward the apex.	5. Nuts longer (20-30 mm. long), commonly conical-ovoid, tapering gradually to the apex.
6. Nuts commonly buff-colored or light yellowish-brown.	6. Color of nuts variable, often light brown to dark brown
7. Cups much more commonly hemispheric or sub-hemispheric than turbinate.	7. Cups as commonly turbinate as hemispheric to shallowly cup-shaped.

often taper to a noticeably thin margin, whereas in the eastern sub-population the thickness is more commonly maintained out to the margin.

Although no one of these is completely constant, this series of differences will usually serve to distinguish between individuals of these two general sub-populations.

Although I have not examined the type specimen of *Quercus turbinella*, illustrations of it (Greene, 1889-90, pl. 27; Trelease, 1924, pl. 206) indicate that it is distinctly more similar to Arizona specimens than to those of California, in the following respects:

1. The oblong to oblong-ovate leaves, with regular spinose dentation and rounded bases, clearly represent the leaf form so commonly encountered in specimens from Arizona and eastward, a form that is rarely duplicated in collections from California (exclusive of the New York Mountains).
2. The fruit is distinctly moderately pedunculate.
3. The nuts are cylindric, tapering abruptly near the apex, rather than conical-ovoid and tapering gradually.

On the other hand, the long acorns and turbinate cups of the type are more characteristic of the Californian sub-

population. Still, either character may occur, albeit infrequently, in Arizona material.

Essentially the same similarities to the eastern sub-population have been noted in every specimen from Lower California examined thus far: San Pedro Martir region, 1902, *Heller* (UC); 45 miles southeast of Tecate, *Munz 9531* (POM); rocky mountains east of Santa Gertrudis, *Purpus 143* (UC); between San Pedro Martir Mission and Santo Tomas, Sierra San Pedro Martir, *Wiggins 9050* (DS); between Ojos Negros and Neji Rancho, *Wiggins & Gillespie 4148* (POM); between Neji Rancho and town of Alaska, *Wiggins & Gillespie 4168* (POM). Plate 208b of Trelease's monograph illustrates still another specimen (Tantillas Mountains, Lower California, 1875, *Palmer 29)* showing essentially these similarities. (Although the plate is captioned "*Quercus dumosa crispata*," the specimen is referred to "*Quercus dumosa turbinella*" as "f. *crispata*" in the text, p. 117.) Moreover, of these specimens, *Munz 9531, Wiggins & Gillespie 4168, Wiggins 9050,* and Trelease's plate 208b all exhibit cup and (or) nut characters that are exactly like those of specimens from Arizona and eastward. It is evident, therefore, that the turbinate cups and elongated nuts which Greene's type exhibits— the two characters which show a resemblance to the Californian sub-population—are not the only forms to be found in Lower California, nor do they seem even to be the most common ones.

Morphologically, therefore, the Lower Californian sub-population differs from the Californian, but is virtually indistinguishable from the eastern sub-population. Geographically, it appears to be isolated from both. [The nearest recorded location in Arizona encountered to date is: Horse Tanks, Castle Dome Mountains, Yuma County, *Benson & Darrow 10839* (POM).] The southern limit of *Quercus turbinella* in California is obscured by gradually increasing intergradation with *Q. dumosa,* as one proceeds southeastward from the region of Cajon Pass in San Bernardino County. This matter will be discussed more fully later in a consideration of the relationship between *Q. turbinella* and *Q. dumosa.* Suffice it to say for the time being, however, that I have seen no specimens truly characteristic of the southern Californian sub-population obtained south or southeast of the area of Morongo Pass, San Bernardino County.

Although the morphological differences between the Californian and mainly extra-Californian sub-populations do not, in my opinion, provide sufficient basis for maintaining the two as distinct species, these differences do suffice to separate them taxonomically as distinct subspecies.

QUERCUS TURBINELLA Greene subsp. **turbinella.** *Q. subturbinella* Trel., Mem. Nat. Acad. Sci. 20: 95, 1924.

Shrub, or infrequently a small shrubby tree to 5 m. tall. Twigs of the current year's growth rather slender, 1–2 mm. in diameter, short yellowish-tomentose, usually densely so, infrequently glabrate. Buds 1–2.2 mm. long, globose to subglobose, glabrescent and reddish-brown. Leaves evergreen, 15–35 (rarely more) mm. long, 10–25 mm. wide, usually oblong or ovate-oblong to ovate, the apex spinosely acute to obtuse, the base rounded to cordate, the lamina not at all decurrent on the petiole, the margin spinose-dentate, the dentation usually quite regular with the teeth often directed outward and forward, gray to grayish-green in color and commonly glaucous; pubescence of microscopic stellate and uniseriate, yellow, glandular trichomes, the former type on both upper and lower surfaces, although less abundant on the upper, the latter type restricted to the lower surface; main secondary veins about 5–7 on either side of midrib, passing into the marginal spines; petioles 2–3 (rarely to 5) mm. long. Fruit annual, usually distinctly pedunculate, the peduncle quite variable in length; cups commonly hemispheric, to infrequently turbinate, rather small, 8–11 (rarely more) mm. in diameter, the cup scales only slightly (or not at all) tuberculate; nuts about 12–23 mm. long, cylindric-ovoid or -ellipsoid, tapering rather abruptly toward the apex, commonly buff-colored or light yellowish-brown.

Type. Twenty or thirty miles below the United States boundary, in Lower California, Mexico. September, 1888, *G. W. Dunn* (Greene-Nieuwland Herbarium, Notre Dame University).

Range. Extending from the Charleston Mountains in southern Nevada, the New York Mountains in eastern San Bernardino County, California, and the higher mountains of northern Lower California, Mexico, eastward through Arizona to western Texas, and presumably into northern Mexico.

Quercus turbinella Greene subsp. **californica** subsp. nov. A *Querco turbinella* subsp. *turbinella* foliis basi rotundatis vel cuneatis rare cordatis in petiolum saepius transeuntibus vel breviter decurrentibus margine plus minusve irregulariter dentatis fructu sessili plerumque longiore (20–30 mm. longo) conico-ovoideo ad apicem versus sensim fastigante discedit.

Differs from typical *Quercus turbinella* in the following characters: the leaf base, although variable in character, is rarely cordate, being rounded to cuneate, the lamina often tapering into or being decurrent for a short distance upon the petiole; dentation of the leaf margin is usually more or less irregular; the fruit is sessile, the nuts are usually longer, 20–30 mm. in length, and are commonly conical-ovoid, tapering gradually to the apex. Other characters in which the subspecies *californica* tends to differ are the following: leaf shape is, in general, more variable—elliptical, sub-orbicular, oblong, or ovate—the apex often more or less rounded; the cups are as

often turbinate as hemispheric, and are often thinner on the margins than in the typical subspecies, and the color of the nut, although variable, is often rather dark brown.

Type. About 2 miles northeast of summit of Caliente Mountain, southeastern San Luis Obispo County, California, October 2, 1948, *Tucker 1886–16* (i.e., no. *16* of the population sample *Tucker 1886)* (UC 938396).

Range. Extending from central San Benito County, California, southeastward in the inner South Coast Ranges to the mountain slopes on or near the southern and western borders of the Mojave Desert in southern California.

Relationship between Quercus turbinella and Q. dumosa

Greene recognized the close affinity of his *Quercus turbinella* to *Q. dumosa,* but was convinced, nevertheless, of the specific distinctness of the two (1889–90; 1890). In his original description of the former, he stated that it occurs "about Campo, in San Diego County" despite the fact that Engelmann had referred earlier collections of his, from the mountains of San Diego County, to *Q. dumosa.*

In my opinion Engelmann was more nearly correct than Greene in his interpretation of the material from San Diego County. The specimens from the vicinity of Campo which I have examined are closer to *Quercus dumosa* than to *Q. turbinella;* these are: 3 miles west of Campo, Dec. 18, 1945, *J. Ashley* (JMT); Campo, *Abrams 3553* (DS); Warren's Ranch, Campo, *Eastwood 9417* (POM); Geo. Meikle's Ranch, Campo, Nov. 1903, *Meikle* (DS, POM). Hence, Greene's inclusion under his new species of material from San Diego County has been a source of long-standing confusion.

Sargent (1895) reduced Greene's species to synonymy, treating the material from Arizona as a form of *Quercus undulata,* and the material from California (and presumably Lower California) as a form of *Q. dumosa.* Jepson (1909 et seq.) treated *Q. turbinella* as a variety of *Q. dumosa.* Abrams originally (1910) regarded them as two distinct species. It is evident, even so, that the latter's concept of *Q. turbinella* was based on specimens (of *Q. dumosa)* from the vicinity of Campo, San Diego County (cf. p. 348, op. cit.). The actual Californian population of *Q. turbinella* he treated as *Q. Alvordiana,* listing it also as a distinct species. In both printings of his later work, "Illustrated Flora of the Pacific States" (1923 and 1940), the same concept of *Q. turbinella* is apparent, although here it is treated as a variety of *Q. dumosa.* By implication, however, he regarded Greene's species (Abrams' *"Q. Alvordiana")* as distinct from *Q. dumosa.*

Within recent years the two extremes of opinion have continued to be voiced, McMinn (1939) regarding *Quercus turbinella* as a form of *Q. dumosa* not worthy of subspecific status,

and Muller regarding the two as distinct species. Muller is aware of the broad area to the east of California where the former is relatively constant and morphologically quite distinct from *Q. dumosa*. Throughout this area, of course, it has no contact with the latter. His conception of the species as it occurs in southern California is that of ". . . an unstable intergrading population tending toward *Q. dumosa* but still representative of *Q. turbinella*" (1940, p. 716).

As we have seen in the preceding section, the Lower Californian sub-population of *Q. turbinella* is isolated geographically (and is subspecifically distinct) from the sub-population of southern California. Similarly, Dr. Ira L. Wiggins has informed me (oral communication) that from his observations in the field there, *Q. turbinella* is apparently completely isolated from *Q. dumosa* (which, however, does occur in northern Lower California). He knows of no area where intergradation occurs between the two. The former occurs along the eastern escarpments of such high ranges as the Sierra San Pedro Martir, as well as in some of the intermontane valleys. The latter occurs at lower elevations in the chaparral of the western coastal slopes. I have seen no specimens from the region that appear to be in any degree intermediate.

The sub-population of southern California is another matter. Here *Quercus turbinella* is the scrub oak component of the pinyon pine-juniper association of arid mountain slopes near or bordering the desert. *Quercus dumosa* is a common element of the slightly more mesophytic interior chaparral subjected, through much of the year, to hot and dry—but not desert—conditions. Although these two oaks intergrade in transitional areas, much of the oak chaparral on the arid desert side of the higher ranges of southern California, particularly northwestward from the region of Cajon Pass, seems to be little or not at all affected. The following are representative specimens of *Q. turbinella* from such areas. San Bernardino Co.: 5 miles east of Big Pine, *Benson 12245* (POM). Los Angeles Co.: road from Rock Creek to Big Pines, *Munz & Johnston 11182* (POM); Big Rock Creek, *Munz 6822* (POM). Kern Co.: Frazier Mountain Park, *Benson 3613* (POM, UC). Ventura Co.: Seymour Creek, Mountain Pinos, *Munz 6985* (POM); Highway 399, 11.9 miles south of junction with Highway 166, *Tucker 1540, 1541* (JMT). Santa Barbara Co.: Salisbury Canyon, Sierra Madre Mountains, *Tucker 1885* (JMT). San Luis Obispo Co.: 2 miles northeast of Caliente Mountain, *Tucker 1886* (JMT).

In addition to the areas mentioned above, in northern Los Angeles, Ventura, and Santa Barbara counties and southeastern San Luis Obispo County, *Quercus turbinella* extends discontinuously northwestward as far as central San Benito County in the inner South Coast Ranges. It also occurs on the western side of the Salinas Valley in Monterey County and on the

desert slopes of the Tehachapi Range. Although through some of these latter areas it intergrades conspicuously with *Q. Douglasii,* its contact with *Q. dumosa* appears to be negligible, and this part of the Californian population will not be considered further here.

A comparison of southern Californian *Quercus turbinella* in its most distinctive state with typical *Q. dumosa* reveals several morphological differences:

TABLE 2. MORPHOLOGICAL DIFFERENCES BETWEEN SOUTHERN CALIFORNIAN QUERCUS TURBINELLA AND Q. DUMOSA.

Q. turbinella	*Typical Q. dumosa*
1. Upper leaf surface gray to gray-green; dull, not shining.	1. Upper leaf surface green and shining.
2. Leaf margin spinose-dentate (teeth with definite short spines to 1 mm. long).	2. Leaf margin usually mucronate-dentate to entire or subspinose; only infrequently definitely spinose.
3. Youngest twigs densely yellow-gray tomentose.	3. Youngest twigs pubescent to glabrate and brownish.
4. Acorn cups thick.	4. Acorn cups thick.
5. Cup scales scarcely (or not at all) tuberculate.	5. Cup scales (especially basal ones) usually strongly tuberculate.
6. Cups turbinate to sub-hemispheric (or deep cup-shaped) but the margins not turning inward.	6. Cups hemispheric to about 2/3 spherical, the margins tapering inward.

In areas of transition between the habitats characteristically occupied by these two oaks, they tend to intergrade. For the purpose of studying this intergradation, three series of population samples were collected along transects across this zone (fig. 2).

The results of this study (which will be reported at a future date) indicate that in areas where *Quercus turbinella* and *Q. dumosa* meet, interbreeding and genic interchange (introgression) have taken place. In the northern part of their zone of contact—in northern Ventura and Los Angeles counties—it is evident, however, that one entity does not merge gradually into the other. Although populations of both have clearly been somewhat modified by introgression, their differences, in general, have not been "swamped out". Even where individuals of both entities occur together in the same immediate habitat, the morphological gap between them is at the most only partially bridged by intermediate forms. In the area of the third transect—Cajon Pass in southwestern San Bernardino County—interbreeding has produced still greater modification in both *Q. dumosa* and *Q. turbinella.*

In addition to these three series of population samples, a number of miscellaneous herbarium specimens of these oaks has been studied. In general, characters of *Quercus dumosa*

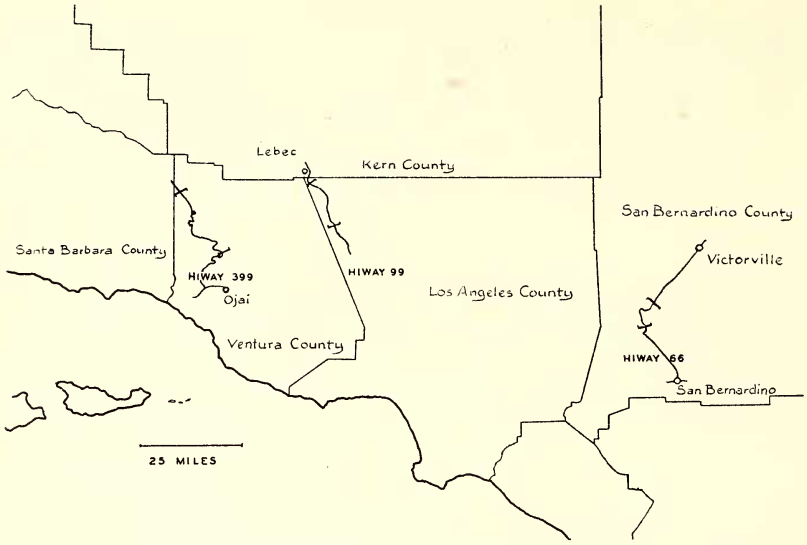

FIG. 2. Location of transects across the zone of intergradation between *Quercus turbinella* and *Q. dumosa*. (Cross-marks on each transect indicate the distance over which population samples were taken, not the extent of the zone of intergradation.)

become more and more prevalent in specimens of *Q. turbinella* from desert slopes eastward and southeastward from the area of Cajon Pass. Indeed, the few specimens seen from the desert mountains of Riverside County, although for the most part intermediate, are, in general, nearer to *Q. dumosa* than to *Q. turbinella*. Most of the specimens from desert border mountains in San Diego County, also, exhibit a preponderance of *Q. dumosa* characters. In my opinion, therefore, this material is best referred to *Q. dumosa*, rather than to *Q. turbinella*.

The typical subspecies of *Quercus turbinella* differs from *Q. dumosa* in all the morphological differences listed in Table 2 except that of cup shape. In addition, the fruit is usually distinctly pedunculate while in *Q. dumosa* it is sessile or subsessile. Moreover, the two taxa occupy quite different ecological situations, and apparently are completely isolated from one another geographically. If only these two entities were involved, taxonomists would probably be unanimous in considering them two distinct species.

The Californian subspecies differs from typical *Quercus dumosa* to a slightly lesser degree perhaps, but in their most characteristic states they are certainly as distinct from each other morphologically as are the members of several other pairs of closely related western oaks (e.g., *Q. dumosa* and *Q. durata; Q. oblongifolia* and *Q. Engelmannii; Q. Garryana* and *Q. Gambelii)*. Characteristically, the two are separated ecologically, also.

It might be argued that the extent of intergradation between *Quercus dumosa* and *Q. turbinella* in southern California is evidence enough that they have not evolved beyond the level of subspecies. The general validity of this argument, as applied in many Angiosperm genera, cannot be denied. It is certainly undeniable, also, that the relationship between the two entities considered here is very close, and that they could be considered conspecific with some justification. However, to regard all entities that are linked by interbreeding as subspecies of a single species is an idea scarcely to be entertained seriously by the student of the genus *Quercus*. My observations and those of others indicate that interbreeding takes place between a number of the Californian white oaks. *Quercus Engelmannii* interbreeds with *Q. dumosa* in southern California, and some of the variability of the latter in Riverside and San Diego counties is probably due to introgression of genic material of the former. *Quercus dumosa* interbreeds with both *Q. durata* (in the foothills of the San Gabriel Range[2]) and *Q. turbinella*. *Quercus turbinella* interbreeds conspicuously with *Q. Douglasii* in the inner South Coast Ranges (Tucker, in press), and *Q. Douglasii* interbreeds with *Q. Garryana* at least locally in northern California (Dobzhansky, 1941). To consider this chain of oaks conspecific on the basis of the lack of clearly defined genetic barriers between them would result in a classification tending more to obscure than to clarify their *phylogenetic* relationships. There seems to be considerable paleobotanical evidence indicating a northern origin for *Q. Garryana* (Chaney, 1944) and a Mexican or southwestern American origin for others, such as *Q. turbinella* (Axelrod, 1940).

Problems of taxonomic status of this sort obviously are matters requiring a consideration of all available evidence and the exercise of careful judgment. Since the degree of morphological difference between typical *Quercus dumosa* and *Q. turbinella* is as great as that between a number of other closely related oaks that are customarily regarded as distinct species, occupy essentially distinct geographical areas, and have different ecological preferences, it is my opinion that the most practicable taxonomic classification is to regard them as two species despite their intergradation in part of their zone of contact.

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[2] In the canyons and lower slopes of the San Gabriel Range north of Pasadena and eastward, the scrub oak population frequently combines the characteristics of both *Q. dumosa* and *Q. durata*. On the basis of herbarium specimens alone, their specific distinctions appear to be completely obliterated. None but a purely arbitrary line of demarcation can be drawn between the infrequent specimens which exhibit a preponderance of *Q. durata* characters and the more common intermediate types which grade into more typical *Q. dumosa*. The scrub oak population as far east as Cajon Pass seems to show, in varying degree, some characters of *Q. durata*.

Quercus Alvordiana

Ever since *Quercus Alvordiana* Eastwood was first described (1905), it has been one of the problematic entities among the Californian oaks. Several different interpretations have been accorded it, and its taxonomic status has varied with different authors. At one extreme has been its recognition as a distinct species, while at the other its existence as an entity worthy of even varietal recognition has been denied.

Sudworth (1908) included *Quercus Alvordiana* in his "Forest Trees of the Pacific Slope," passing over it very briefly but noting an apparent close relationship with *Q. dumosa.* Jepson, in his "Flora of California" (1909), reduced *Q. Alvordiana* to a variety of *Q. dumosa,* and accorded it the same treatment in his later works (1910, 1925). Abrams (1910, 1923 & 1940) assigned *Q. Alvordiana* specific rank, but his concept was evidently based on *Q. turbinella.* Trelease (1924) cited *Q. Alvordiana* under *Q. dumosa* as "f. *Alvordiana* Jepson, Silva Calif., p. 218, 1910." (This is an erroneous citation; to my knowledge, this combination was never published by Jepson.) Munz (1935) followed Jepson in treating *Q. Alvordiana* as a variety of *Q. dumosa.* McMinn (1939) listed *Q. Alvordiana* under *Q. dumosa* without according it even varietal status. He made the interesting observation that "In the inner South Coast Ranges from the San Carlos Range to the San Emigdio Mountains of Kern County this species [*Q. dumosa*] apparently hybridizes with *Q. Douglasii,* . . ." This is an observation of special significance in any consideration of *Q. Alvordiana.*

The original description of *Quercus Alvordiana* is brief and in very general terms, and includes several points that might apply as readily to *Q. turbinella* (with which it has been confused) as to the type. A more important factor contributing to the confusion has undoubtedly been the illustration (op. cit., pl. 27, fig. 4) accompanying the description—a photograph of a small twig bearing several leaves and an acorn. This figure closely simulates *Q. turbinella* of southern California, although the acorn is somewhat longer than is characteristic for the latter. Examination of the actual twig (filed with the type specimen, CAS 1034) confirms this. Indeed, upon the back of the envelope in which the twig is kept, appears the inscription in Miss Eastwood's handwriting: *"Quercus turbinella!"* Obviously, then, the original description of *Q. Alvordiana* was illustrated with a specimen that is scarcely distinguishable from *Q. turbinella.*

The type specimen (fig. 3), on the other hand, is distinctly different from *Quercus turbinella* in several characters: (1) the upper leaf surfaces are darker in color, (2) the leaf margins, although often dentate, tend to be fairly smooth (not at all spinose as in *Q. turbinella),* and some leaves are nearly or quite entire, and (3) the buds are ovoid rather than globose or sub-

FIG. 3. Type specimen of *Quercus Alvordiana*.

globose. Aside from the small leaf size and characters of the acorns—which are points of similarity to *Q. turbinella*—this specimen is much closer to *Q. Douglasii*. Taking all its characters into account, it could be considered aberrant *Q. Douglasii*. There would seem to be little doubt, then, that the type specimen and the twig photographed for the illustration represent material from two quite different individuals.

The type was collected by Eastwood in San Emigdio Canyon, Kern County, California, October 2, 1894. In what is evidently the original inscription on the label, the specimen was named "*Quercus dumosa* Nutt." and described as a "small tree." Another inscription occurs on the label along its upper margin: "*Quercus Douglasii*, fide Sargent"; a third occurs beside the label on the sheet itself: "*Quercus Alvordiana* Eastwood Type." All three are in Miss Eastwood's handwriting, and each is written in a different type of ink, suggesting a different time of writing for each. Thus, apparently the specimen was first regarded as *Quercus dumosa* by Eastwood, then following C. S. Sargent, as *Q. Douglasii*, and finally, as a new species, *Q. Alvordiana*, with this specimen as type. I have seen ten different Eastwood collections (from the Herbarium of the Arnold Arboretum) from San Emigdio Canyon, all but two of which bear the same date as the type. Morphologically they represent a series of forms ranging from slightly aberrant *Q. Douglasii* (no. *72:* "largest tree of the kind seen in the canyon"), through several intermediate forms (nos. *122*—an isotype, *123*, and *74;* all described as small trees), to individuals of *Q. turbinella* (nos. *120*, *121*, and Mar. 27, 1893, *Eastwood sine no.*).

Eastwood recognized several of these specimens as *Quercus Douglasii* judging by the names on their labels. In considering the several intermediate forms, it is interesting to note Sargent's statement that ". . . in the herbarium it is not always easy to distinguish some of the southern forms of this species [*Q. Douglasii*] from the green-leaved *Quercus dumosa*, and Miss Eastwood suggests that natural hybridizing between these trees would account for the apparent running together of the two species . . ." (1895, 8: footnote, p. 79). No mention of hybridization is made, however, in the original description of *Q. Alvordiana,* nor any mention of its affinities to other species.

Previous to studying these collections from the type locality, however, I had gained an impression from several sources that *Quercus Douglasii* and *Q. turbinella* were involved in the makeup of *Q. Alvordiana*. (The binomial, *Quercus Alvordiana*, is being used only for convenience of reference; I do not accord this entity the status of species.) Most revealing were observations made in the Vegetative Type Map Herbarium, Berkeley, several years ago. A number of specimens had been noted which were intermediate in varying degrees between *Q. Doug-*

lasii and *Q. turbinella,* some being more like one, others more like the other. The specimens with larger and darker-colored leaves had been identified as *Q. Douglasii,* those with smaller leaves had been named *Q. dumosa* (although, according to their collection data, most of them were trees, e.g., *T. M. Hendrix 215:* tree 35 feet tall, 18 inches in trunk diam. at breast height) or *Q. dumosa* var. *Alvordiana,* and a number had been filed in the "undetermined" folder with no specific name at all. For the most part they were from the inner South Coast Ranges, the western side of the Salinas Valley in southern Monterey County, and the Mount Pinos area (including San Emigdio Canyon).

The postulate was made that *Quercus Alvordiana* has arisen through interbreeding between *Q. Douglasii* and *Q. turbinella.* Rather than follow the narrow practice of applying the name *Quercus Alvordiana* only to forms that resemble the type specimen more or less closely, a broader concept was adopted, under which this name is used in reference to intermediate populations, and the intermediate individuals of mixed populations (in which individuals of *Q. Douglasii* and *Q. turbinella* occur).

In order to test this hypothesis, a series of population samples was collected in a number of areas in the range of *Quercus Alvordiana* (essentially the areas where the ranges of *Q. Douglasii* and *Q. turbinella* overlap) as well as in areas where the presumed parental species occur far removed from one another geographically. A total of 39 such collections was made. For their analysis, a "hybrid index" (Anderson, 1936) was constructed, based on a number of the most constant differences between *Q. Douglasii* and *Q. turbinella* as determined from an extensive series of miscellaneous herbarium specimens.

TABLE 3. MOST CONSTANT DIFFERENCES BETWEEN QUERCUS TURBINELLA AND Q. DOUGLASII.

Quercus turbinella	*Quercus Douglasii*
1. Shrub, rarely a small shrubby tree (to 5 m. tall).	1. Tree, medium-sized to rather small (7 m. tall).
2. Mature terminal buds globose to subglobose.	2. Mature terminal buds ovoid to broad-ovoid.
3. Mature leaves 15-35 (rarely 40) mm. in length.	3. Mature leaves 30-70 (rarely 90) mm. in length.
4. Leaf margins spinose-dentate.	4. Leaf margins crenate-dentate or -lobed to entire.
5. Color of upper leaf surface gray to grayish-green.	5. Color of upper leaf surface bluish-green.
6. Stellate trichomes of lower leaf surface with 7 or more (commonly 8) rays.	6. Stellate trichomes of lower leaf surface with 5 or fewer (commonly 4) rays.

The results of this study of population samples (Tucker, in press) are definitely in accord with the postulate stated above. In areas distant from their region of geographical overlap, *Quercus Douglasii* and *Q. turbinella* are very distinct from one another morphologically. In areas where they occur together in the same habitat, the common occurrence of an array of forms which are morphologically intermediate between the two in varying degrees, furnishes circumstantial evidence of interbreeding between them. At least one such population has been encountered at the type locality, San Emigdio Canyon, Kern County. Occasional populations are encountered, however, that are more homogeneous, but which are, in general, more or less intermediate. This type of population may resemble either one species or the other more closely, or it may be very nearly midway between them. The general range of this series of mixed and intermediate populations is as follows: hills along the west side of the Salinas Valley in Monterey County, inner South Coast Ranges from central San Benito County southward to the northern slopes of the Mount Pinos region, desert slopes of the Tehachapi Range, and the hills bordering Antelope Valley north of the Liebre Range, in northwestern Los Angeles County.

Corroborating evidence has been furnished by a field study of the relative length of leaf persistence in the various entities involved. *Quercus Douglasii* is deciduous, *Q. turbinella* is evergreen, and *Q. Alvordiana* is more or less intermediate between these conditions.

The available paleobotanical and geological evidence, although scanty, seems to support the hypothesis. This is discussed elsewhere (Tucker, in press).

The diversity of this series of populations and its lack of distinctness from *Quercus Douglasii* on the one hand and *Q. turbinella* on the other, result in a situation which is highly problematic for the taxonomist. Two questions are involved: (1) To what latitude of forms should the name *Quercus Alvordiana* be applied? (2) What is the best taxonomic status for this entity?

In a consideration of the first question, it would seem more logical to apply Eastwood's name to all forms intermediate between *Quercus Douglasii* and *Q. turbinella,* rather than just to forms that more or less closely resemble the type, for the following reasons. In San Emigdio Canyon, the type locality of *Q. Alvordiana,* interbreeding between *Q. Douglasii* and *Q. turbinella* is clearly indicated by the occurrence of intermediates which almost completely bridge the morphological gap between these two species. Moreover, Eastwood's type is intermediate to a degree, although in general it is distinctly closer to *Q. Douglasii.* It may well be that Eastwood's intention in publishing *Q. Alvordiana* as a new species was to call attention